23. On the Persistence of the Mesopterygoid in certain Reptilian Skulls. By R. Broom, F.R.S., C.M.Z.S.

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(Text-figures 5–7.)

In 1878, Kitchen Parker described the structure and development of the skull in the Common Lizard, and figured a section of a fairly advanced *Zootoca* showing the region where the pterygoid articulates with the basisphenoid. A fairly large intercalary cartilage is shown to be present, but Parker apparently did not consider it to be of any important morphological value.

In 1901, Howes and Swinnerton described the development of the skull of *Sphenodon punctatus* (Trans. Zool. Soc. xvi. p. 1. 1901), and showed that there is also a cartilage similar to that noticed by Parker in *Zootoca*, interposed between the pterygoid and the pterygoid process of the basisphenoid. They compare it to the meniscus found in the articulation of the jaws of most mammals, and give to it the name *meniscus pterygoideus*.

For many years I have been inclined to think that this little cartilage would yet turn out to be of considerable morphological importance, but until recently I have never been able to get any clear light on it from either skeletogenesis or palæontology. Within the last few years, however, two papers have appeared which seem to show with hardly any doubt that this little *meniscus pterygoideus* of Howes and Swinnerton is really a persistent piscine mesopterygoid.

Before discussing the nature of the element, it will be well to consider in some detail its structure and relations, as, so far as I am aware, it has never hitherto been at all fully described or figured.

Among living animals it is only known to occur in Lizards and *Sphenodon*, and as it can be seen even better in the primitive Lacertilian *Agama* than in *Sphenodon*, I will give a few figures of it as it occurs in a larval *Agama hispida*.

Text-fig. 5 represents a graphical reconstruction of the middle part of the base of the skull of the embryo *Agama* with a skull length of 7 mm.* The membrane bones of the skull are all ossified at this stage, but in the cartilage elements, such as the quadrate, ossification has just started as an exostosis. As is seen in the figure given, the pterygoid is well ossified, and extends far forward, though it does not meet the prevomer as in *Sphenodon*. The basicranial cartilages are still unossified, and from the basisphenoid region there passes outwards a well-developed basipterygoid process to support the pterygoid; but it will be seen that it only supports the pterygoid indirectly, as a large independent cartilage lies between the basipterygoid process and the pterygoid. This is the *meniscus pterygoideus* of Howes and Swinnerton, and the element whose affinities we wish to examine. It is rather longer than the face of the basipterygoid process, and, as will be seen in the cross-sections given, it is of considerable thickness. It completely separates the pterygoid from the basisphenoid, so that no part of the pterygoid is in contact with the basicranial cartilage. Further, the "meniscus" has no direct relations with the epipterygoid, the pterygoid completely separating the one from the other. To a considerable extent it is clasped by the pterygoid, and the movement at the joint is between the "meniscus" and the basipterygoid process and not between the pterygoid and the "meniscus." In fact, it is pretty manifest from the examination of this embryo alone that the element is really a pterygoid element.

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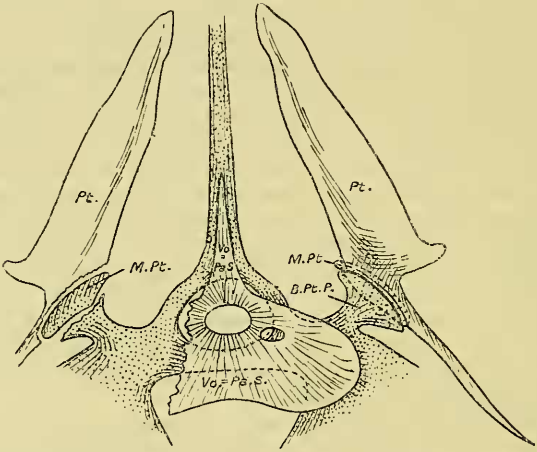
* I am indebted to Prof. J. P. Hill for having kindly sectioned the *Agama* skull for me.

Text-figure 5.



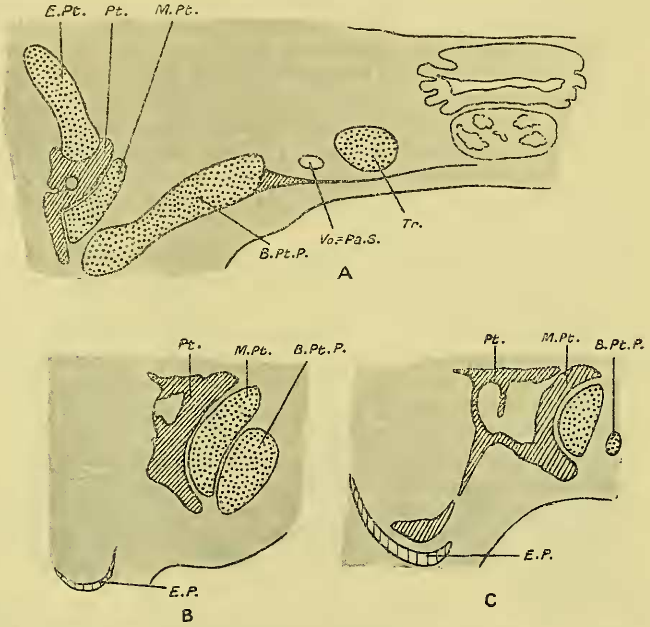
Base of skull of embryo *Agama hispida* var. *aculeata*. Head length 7 mm. Reconstructed from sections. On the right side, parts of the vomer (parasphenoid), basipterygoid process, and of the pterygoid have been removed; and a full view is given of the mesopterygoid.

References to lettering in figures:—*B.Pt.P.* Basipterygoid process of Basisphenoid; *E.P.* Ectopterygoid (in *B* & *C* of fig. 6 the element is not yet ossified where sectioned); *E.Pt.* Epipterygoid; *M.Pt.* Mesopterygoid; *Mx.* Maxilla; *Pa.* Palatine; *Pmx.* Premaxilla; *Pt.* Pterygoid; *P.Vo.* Prevomer; *Q.* Quadrate; *Tr.* Trabecula; *Vo=PaS.* Vomer=Parasphenoid.

The reconstruction of the base of the skull in this *Agama* embryo shows a very interesting condition of the median basal bony element which the large majority of morphologists call the parasphenoid, but which I regard as the true homologue of the mammalian vomer. Besides nearly covering over the pituitary opening, it forms a large support to the basisphenoid cartilage, especially in the neighbourhood of the basipterygoid process. In front this median vomer or "parasphenoid" extends forward as a support to the median septum almost exactly as does the mammalian vomer.

The fossil Tetrapod skull that has given us the clue to the real affinity of the "meniscus" is that of "*Seymouria baylorensis*" Broili, recently described by Watson. "*Seymouria*" is one of the most interesting primitive fossil types ever discovered; and Broili, Williston, and Watson have revealed to us nearly every detail of its structure. There are, however, two points on which one would like to remark. Williston, v. Huene, and Watson all agree that *Seymouria baylorensis* Broili is the same animal as *Conodectes favosus* Cope. Cope's type skull is in the American Museum, and his description, though by no means such as would enable anyone to identify readily a similar species, is fuller than that of many types, and I cannot agree with Watson that Cope's

Text-figure 6.



Transverse sections through the mesopterygoid and related elements in the skull of the embryo *Agama* shown in Fig. 5.

A. Through the posterior part of the element.
B. A section near the middle.
C. A section near the anterior end.

name should be treated as a *nomen nudum*. *Conodectes* has eight years' priority over *Seymouria*, and if those who have examined both types are satisfied that they belong to the same species, I think we will have to use Cope's name *Conodectes favosus* in preference to that of Brioli.

The second point is a much more debatable one. Watson describes "*Seymouria*" as "the most primitive known reptile," and everyone else who has written about the animal has also been of the opinion that it is a reptile; and until Watson's paper appeared, I also accepted this opinion, having never seen any of the actual specimens. I do not in the present paper wish to enter at length into the discussion, but may state that the study of Watson's paper leads me rather to the conclusion that *Conodectes* is a highly evolved and specialized Embolomerous Amphibian, with a very few reptile-like characters which have been acquired by a parallel development. For the present, however, it matters little whether *Conodectes* is an Amphibian-like Reptile or a Reptile-like Amphibian. It certainly lets us know more of the primitive Tetrapod structure than almost any other known type, and fortunately the palate is well known, and has been fully described by Watson.

There is a large pterygoid which meets its neighbour in front, and it is supported indirectly by a basipterygoid process. Between the process and the pterygoid is a distinct bony element, concerning which Watson says:—"The short basipterygoid processes of *Seymouria* supporting the pterygoid through the intervention of a special bone are unique, nothing similar occurring in any other known adult reptile or amphibian. The shape and position of the pterygoid render it certain that these special bones cannot be the epipterygoids, which in *Dimetrodon* are known to articulate with the basisphenoid. Swinnerton and Howes showed that in the development of the skull of *Sphenodon* special articular cartilages are developed between the basipterygoid processes and the pterygoid, and it is not impossible that these are the representatives of the articular bones in *Seymouria*.

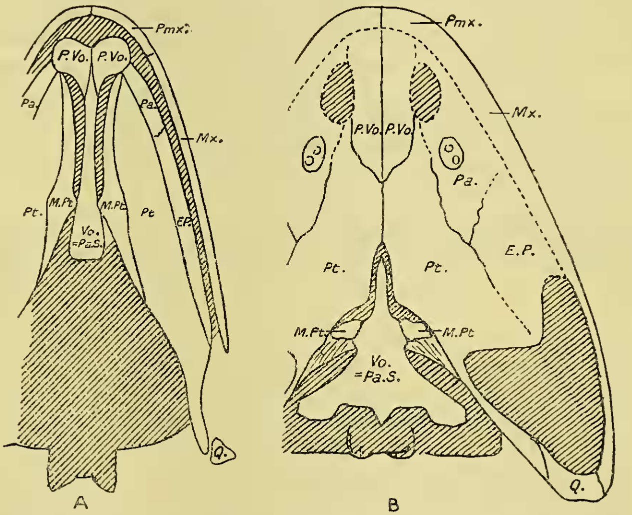
"On the other hand, Gaupp has shown that in *Lacerta* the basipterygoid processes contain independent centres of ossification, and it is feasible and attractive to regard the *Seymouria* bones as permanently separate autogenous basipterygoid processes."

With regard to this second suggestion, it may be mentioned that the basisphenoid in lizards and many other animals ossifies for the most part from the parasphenoid, and, so far as I am aware, no one has confirmed Gaupp's observation. Parker examined an embryo *Zootoca* (his 6th stage) which one would fancy ought to show the basipterygoid distinct if it is ossified from a separate centre; but there is no evidence of this. Howes and Swinnerton figure a stage in the development of the skull of *Sphenodon* (stage 8) where the basisphenoid is evidently ossified from a pair of centres each of which embraces the basipterygoid process. If Gaupp's observation be confirmed, the ossifications must be regarded, I think, as the paired centres of the true basisphenoid. In fact, if one looks at the basisphenoid of an embryo lizard with its huge median fontanelle (*cf.* text-fig. 5), it is difficult to see how it could be ossified except by lateral ossifications if it is not completely ossified by invasion from the parasphenoid.

The other suggestion made by Watson, that the *meniscus pterygoideus* found in *Sphenodon* by Howes and Swinnerton and previously figured by Parker in the lizard is the homologue of the little bones in "*Seymouria*," seems to me manifestly the correct one.

The bony element which forms the cranial base is regarded by Watson as made up of parasphenoid in front and basisphenoid behind. Though I have not seen the specimens, I incline to think it probable that the whole will prove to be parasphenoid or vomer. But, in any case, there seems to me no doubt that the little intercalated element is the homologue of the little one we have in the lizard and *Sphenodon*.

Text-figure 7.



A. The palate of the Rhipidistian Fish, *Eusthenopteron foordi*. After Bryant.

B. The palate of the primitive Tetrapod *Conodectes favosus* Cope=*Seymouria baylorensis* Broili. After Watson. In the opinion of Watson, Williston, and others this is a very primitive reptile: the writer favours the view that it is a highly developed Embolomerous Amphibian.

When we go further down in the scale we have hitherto had difficulties, as no good palate was known of any of the Rhipidistian

Crossopterygians. Now, however, this difficulty has been removed by the description of the palate of *Eusthenopteron foordi* by Bryant*, and we have the clue to the little element in both *Conodectes* and the lizards (text-fig. 7). As will be seen from the figure, there is a large bone which has on its outer side a palatine, and an ectopterygoid, and which is manifestly the pterygoid of the higher forms. Internally it articulates with a long, slender bone which is the mesopterygoid of the bony fishes. This mesopterygoid is supported by the parasphenoid or vomer. The relations of all the bones is very similar to what we have in the higher forms, and the only striking difference is that in the Tetrapods the mesopterygoid has become greatly reduced and usually lost. But when it is retained it is found, as in the Rhipidistian fish, supporting the pyterygoid and itself articulating with the basipterygoid process of the basisphenoid or the parasphenoid.

There is one other group of fossil reptiles in which it is possible there is also a distinct mesopterygoid. Sollas†, in describing recently the skull of *Ichthyosaurus* from serial sections, showed that there are two epipterygoid-like elements on each side. The posterior pair are, I think, manifestly the true epipterygoids. Not improbably the anterior pair will prove to be mesopterygoids, which in the specimen examined by Sollas had been slightly displaced outwards by crushing.

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* "On the structure of *Eusthenopteron*," Bull. Buffalo Soc. Nat. Sci. xiii. pp. 1–59 (1919).

† "The skull of *Ichthyosaurus*, studied in serial sections," Phil. Trans. vol. 208 B (1916).